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Four new species of forest-dwelling mantellid frogs from Madagascar allied to *Gephyromantis moseri*

(Amphibia, Anura)

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The *Gephyromantis moseri* complex, classified in the mantellid subgenus *Duboimantis*, currently contains one species of frog, *G. moseri* (Glaw & Vences, 2002) from the Andasibe area in the Northern Central East of Madagascar, as well as several genetically divergent populations from the North East that have been provisionally assigned to the species. We here analyse DNA sequences of one mitochondrial (16S rRNA) and one nuclear-encoded gene (RAG-1), morphology, and advertisement calls of newly collected material of this species complex from various localities in Madagascar. Based on this integrative evidence, in particular concordant nuclear gene differentiation between seven highly divergent (>4 %) mitochondrial lineages, as well as differences in advertisement call structure, body size and head shape between some of these lineages, we conclude that the *G. moseri* complex contains several additional species of which four are formally named and described in this study: *G. fuscus* sp. nov., a rather small-sized species sister to *G. moseri*, occurring in two sites (Mahasoa and the western part of the Makira Reserve), *G. makira* sp. nov., a species known from only one available voucher specimen from eastern Makira, *G. bemiray* sp. nov. from eastern Makira, Masoala, and Ambolokopatrika; and *G. ampondo* sp. nov. from Marojejy in the North East. Two further lineages for which voucher specimens were not available in the framework of this study are considered unconfirmed candidate species *G.* sp. Ca19 and *G.* sp. Ca33, pending the collection of further material. The revision of the *G. moseri* complex adds to the diversity of *Duboimantis* and once more demonstrates the existence of secretive or genuinely rare restricted-range species among the Malagasy frogs whose inventory can only be completed by further fieldwork and integrative taxonomic research.

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Introduction

With 58 species currently recognized (AmphibiaWeb 2023), *Gephyromantis* is one of the largest and most diverse genera in the Madagascar/Comoro-endemic anuran family Mantellidae. *Gephyromantis* predominantly occur in the rainforests of eastern and northern Madagascar, with one subclade (subgenus *Phylacomantis*) mostly inhabiting the more arid western parts of the island. Although a few species appear to be specialized to humid montane forests at elevations of 1500–1800 m a.s.l. (e.g., *G. cornucopia*, *G. tohatra*; Scherz et al. 2017a, Miralles et al. 2023), no *Gephyromantis* are known from truly montane habitats such as heathlands and grasslands above the tree line at elevations >2000 m a.s.l. on Madagascar's highest massifs.

Recent years have seen an enormous increase in species descriptions of *Gephyromantis*, facilitated by integrative approaches relying on DNA sequence data, but also on the obvious bioacoustic differentiation among many of the newly discovered *Gephyromantis* species (e.g., Vences et al. 2003, Glaw & Vences 2011, Glaw et al. 2011, Vieites et al. 2012, Wollenberg et al. 2012, Scherz et al. 2017a,b, 2018a,b, Vences et al. 2021, 2022, Hutter et al. 2022, Miralles et al. 2023). Despite these efforts, large-scale molecular screening indicated that yet more new species await revision and formal description (Vieites et al. 2009, Perl et al. 2014). Aligned with the situation in many other components of Madagascar's biota (Wilmé et al. 2006, Vences et al. 2009), many *Gephyromantis* species are microendemic, i.e. restricted to very small ranges in Madagascar, while other species are more widespread and often contain geographically restricted deep intraspecific genetic lineages.

Of the six subgenera of *Gephyromantis* (Glaw & Vences 2006, Vences et al. 2017), the subgenus *Duboimantis* is perhaps the most prominent one in Madagascar's rainforest. *Duboimantis* are relatively large-sized species that are very vocal at night, typically calling from perches on trees and bushes, and can regularly be observed active in the leaf litter of the forest floor during the day. Taking into account the latest species descriptions (Scherz et al. 2018b, Vences et al. 2021b), *Duboimantis* currently contains 16 species, with a center of species richness in northern Madagascar (Kaffenberger et al. 2012), but also including species endemic to the Northern Central East and Southern Central East (regions after Boumans et al. 2007, Brown et al. 2016). One of these species is *Gephyromantis moseri*, a species originally described by Glaw & Vences (2002) in the genus *Mantidactylus*, from near Andasibe, one of the regions of highest amphibian species richness in Madagascar. Among *Duboimantis*, *G. moseri* is a poorly known species that is rarely collected, and it is uncertain whether this reflects secretive behaviour, rareness, or patchy distribution. Populations assigned to *G. moseri* are known from several sites in Madagascar, extending from Andasibe to Marojejy in the North East (Glaw & Vences 2002, Glaw & Vences 2007, Rosa et al. 2012), but initial assessments indicate that these are genetically highly diverged, and that *G. moseri* may constitute a species complex (Vieites et al. 2009, Kaffenberger et al. 2012, Perl et al. 2014).

In this study, we assembled new samples of the *G. moseri* complex from various sites across its range and analyse newly determined mitochondrial and nuclear DNA sequences, as well as advertisement call recordings and morphological differentiation across the known populations of this complex.

Materials and methods

We aimed to analyse all voucher specimens, samples and call recordings of the *G. moseri* complex available to us. This included material that was part of the species' original description (Glaw & Vences 2002), as well as subsequent collections from Andasibe, Ambolokopatri-

ka, Mahasoa, Makira, Masoala, and Marojejy. During fieldwork at these sites, frogs of the *G. moseri* complex were collected either opportunistically during the day when encountered on the forest floor, or at night with the aid of torchlights, most often in targeted searches of calling male specimens. Collected specimens were anaesthetised and subsequently euthanised by immersion in aqueous solution of tricaine methanesulfonate (MS222) or chlorobutanol. Tissue samples for molecular analysis were taken from the euthanized specimens and stored separately in 1.5 ml vials with 95% ethanol. Vouchers were then fixed in 95% ethanol or in 4% formaldehyde solution, preserved in 70% ethanol, and deposited in the Biodiversity Institute and Natural History Museum of the University of Kansas (KU); Zoologisches Forschungsmuseum A. Koenig, Bonn (ZFMK); Museo Regionale di Scienze Naturali, Torino (MRSN); Zoological Museum Amsterdam (ZMA; collection now included in Naturalis, Leiden); Zoologische Staatssammlung München (ZSM); and the Université d'Antananarivo, Mention Zoologie et Biodiversité Animale (UADBA). FGZC, FGMV and ZCMV refer to field numbers of F. Glaw and M. Vences. FAZC and FN refer to field numbers of F. Andreone. CRH, APR, MSZC and ACZCV refer to field numbers of C. R. Hutter, A. P. Raselimanana, M. D. Scherz and A. Crottini, respectively. Geographic regions within Madagascar are named according to Boumans et al. (2007) and Brown et al. (2016).

Morphometric measurements of voucher specimens were taken by MV with a manual caliper and an accuracy of 0.1 millimeter, as follows: snout–vent length (SVL); maximum head width (HW); head length from tip of snout to posterior edge of mouth opening (HL); horizontal tympanum diameter (TD); horizontal eye diameter (ED); distance between anterior edge of eye and nostril (END); distance between nostril and tip of snout (NSD); distance between both nostrils (NND); forelimb length, from limb insertion to tip of longest finger (FORL); hand length, from the articulation of the carpals with the radioulna to the tip of the longest finger (HAL); hindlimb length, from the cloaca to the tip of the longest toe (HIL); foot length (FOL); foot length including tarsus (FOTL); and tibia length (TIBL). Webbing formula is reported according to Blommers-Schlösser (1979) to ensure comparability with previous species descriptions of Malagasy frogs.

We recorded vocalizations in the field using a tape recorder (Tensai RCR-3222) with an external microphone (Vivanco EM 238), and with digital recorders with built-in microphones (Edirol R-09 or iPhone 12 Pro). Recordings were sampled or re-sampled at 22.05 kHz and 32-bit resolution and analysed using the software Cool Edit Pro 2.0. We obtained frequency information through Fast Fourier Transformation (FFT; width 1024 points) at Hanning window function. Spectrograms were produced at Blackman window function with 256 bands resolution. In some cases, filtering was used to remove background sounds, applied only to frequencies outside the prevalent bandwidths of calls. Temporal measurements are summarized as range with mean ± standard deviation in parentheses. Terminology and methods in call analyses and their descriptions follow the recommendations of Köhler et al. (2017). Call recordings were deposited at the Zenodo repository (DOI: 10.5281/zenodo.10278042).

To assess genetic divergence between individuals and lineages of the *G. moseri* complex, we PCR-amplified and sequenced DNA fragments of two genes, one mitochondrial-encoded (16S rRNA) and one nuclear-encoded (Recombination-activating gene 1, RAG-1). DNA was salt-extracted (Bruford et al. 1992) and subsequently, the following combinations of primers and PCR conditions used: 16SFrogL1/16SFrogH1 (5'-CATAATCACTTGTTCTTTAAA-3'; 5'-GATCCAACATCGAGGTCG-3') modified from Palumbi et al. (1991), with the following PCR protocol: initial denaturation for 90 s @ 94 °C, followed by 36–40 cycles of denaturation for 45 s @ 94 °C, primer annealing for 45 s @ 50–53 °C and elongation for 90 s @ 72 °C, followed by a final extension step for 5 min @ 72 °C. For RAG-1, we used the primers Gephlut-RAG1-F1 (5'-ATGGAGAGCCAACCCCTATC-3') and Gephlut-RAG1-R1 (5'-KCCAGACTCGTTTCCTTCRC-3') (Vences et al. 2021b) with the PCR protocol: 120 s @ 94 °C, 35 x [20 s @ 94 °C, 50 s @ 53 °C, 180 s @ 72 °C], 600 s @ 72 °C.

PCR products were purified with Exonuclease I and Shrimp Alkaline Phosphatase digestion, and sequenced by LGC Genomics (Berlin) on an automated capillary sequencer. Chromatograms were checked for base-calling errors and edited with CodonCode Aligner 6.0.2 (Codon Code Corporation, Dedham, MA, USA) and newly determined sequences submitted to GenBank (accession numbers OR913525–OR913547 and OR920355–OR920372).

Sequences were aligned for each locus in MEGA7 (Kumar et al. 2016) with the Clustal alignment option. As the alignment was unambiguous and only required few indels for 16S (especially in the outgroup), all sites were used for phylogenetic analysis. All alignments and a table with metadata of voucher specimens (including sequence accession numbers) are available from the Zenodo repository (DOI: 10.5281/zenodo.10278042).

We analysed the 16S data set using Maximum Likelihood inference in MEGA 7 under a Tamura-Nei + Gamma substitution model selected using the Bayesian Information Criterion with SPR branch swapping, and 500 nonparametric bootstrap replicates to assess node support. For an objective inference of primary species hypotheses, we used ASAP (Puillandre et al. 2021) as implemented in iTaxoTools (Vences et al. 2021a). Pairwise sequence distances between ASAP-inferred lineages were then calculated using the program TaxI2 (Vences et al. 2021a). For ASAP and TaxI2, we used a reduced and trimmed alignment of 490 bp containing 32 sequences with less than 22 missing nucleotides (i. e., removing one sequence with a large number of missing data). We used the same reduced 16S dataset, complemented with a full-length 16S sequence of *Mantella baroni* (Kurabayashi et al. 2008), to determine molecular diagnostic sites for the inferred species in the *G. moseri* complex using MolD (Fedosov et al. 2022) (alignments available from the Zenodo repository, DOI: 10.5281/zenodo.10278042).

The RAG-1 alignment was analysed separately from the 16S dataset to understand concordance (or absence thereof) in the differentiation of these two unlinked genetic markers. We used a haplotype network visualization to graphically represent the relationship among RAG-1 alleles (haplotypes). Haplotypes were estimated with the PHASE algorithm (Stephens et al. 2001) implemented in ConvPhase, and a haplotype network using the TCS algorithm (Templeton et al. 1992) was constructed in Hapsolutely (part of iTaxoTools).

As in previous studies, we follow the general lineage concept (de Queiroz 1998, 2007) in combination with a relaxed biological species criterion, i.e., demanding reproductive isolation indicated by restricted gene flow among lineages (e.g., Speybroeck et al. 2020). Because reproductive barriers generated through time increase genealogical depth and agreement among unlinked loci (Avise & Wollenberg 1997), we use genealogical concordance (Avise & Ball 1990) between mitochondrial and nuclear loci, especially in populations occurring in sympatry or close geographical proximity, as an indicator for restricted gene flow. Species status is then assigned to lineages based on combined evaluation of genetic, morphological and bioacoustic evidence (Padial et al. 2010).

Results

Phylogeny and molecular differentiation

The final 16S alignment contained 33 ingroup sequences for 490 bp. The ML analysis (Fig. 1) revealed a tree with a basal trichotomy of three major clades: one (bootstrap support BS = 54 %) containing various subclades from Mahasoa and Makira West, Makira East 900 m, and Andasibe + Betampona; a second clade (BS = 94 %) with samples from Masoala, Ambolokopatrika, Makira Simpona Lodge, and Makira Andaparaty; and a third clade (BS = 82 %) with samples from Marojejy, Ambolokopatrika, and Masoala (see Fig. 2 for distribution of the lineages). The three main clades and several of the subclades were separated by relatively long branches, and defining main lineages for comparison and further analysis was therefore not trivial. ASAP calculated a species partition with as many as 12 ingroup subsets as the preferred solution (with the lowest ASAP score = 3.5) and partitions with the second to fifth lowest ASAP scores (5.0–6.0) suggested 10–17 subsets. Since these solutions contained obvious taxonomic inflation (e.g., specimens from Angozongahy at the western slope of the Makira Plateau, collected at the same site emitting extremely similar advertisement calls, were grouped in different subsets), we chose the 9th best partition with seven subsets (ASAP score = 8.0) as the basis for further analysis, and labelled samples in the tree (Fig. 1) accordingly. The seven subsets correspond to the following lineages (Fig. 2): (i) *G. moseri* from Andasibe and Betampona; (ii) a lineage from Mahasoa and the western slope of Makira previously named *G.* sp. Ca22 and herein described as *G. fuscus* sp. nov.; (iii) a lineage from Makira herein described as *G. makira* sp. nov.; (iv) a lineage from Marojejy herein described as *G. ampondo* sp. nov.; (v) a lineage from Ambolokopatrika, Makira, and Masoala, previously named as *G.* sp. Ca18 and herein described as *G. bemiray* sp. nov.; (vi) a lineage from Ambolokopatrika and Masoala previously called *G.* sp. Ca19; and (vii) a lineage from Masoala newly discovered in this study for which we coin the new candidate species number *G.* sp. Ca33. In the following, we already use the new species names to avoid having to refer to the lineages using preliminary OTU or candidate species names, anticipating the taxonomic conclusions that we will formalize in the subsequent species accounts.

Pairwise uncorrected distances (p-distances) in the 16S fragment were high among the seven lineages (Table 1). The lowest average distances of 4.5–5.5 % were found among *G. moseri*, *G. fuscus* sp. nov. and *G. makira* sp. nov., and between *G. ampondo* sp. nov. and *G.* sp. Ca19, whereas distances were at least 6.0 %, and up to 9.8 %, in all other comparisons.

Table 1. Mean uncorrected pairwise distances (p-distances), with minimum and maximum values in parentheses, in % among and within lineages in the *Gephyromantis moseri* complex, calculated from a 490 bp alignment of the 16S rRNA gene. NA, not applicable.

	G. moseri	*G. fuscus* sp. nov.	*G. makira* sp. nov.	*G. ampondo* sp. nov.	*G. bemiray* sp. nov.	*G.* sp. Ca33	*G.* sp. Ca19
G. moseri	0.4 (0.0–0.8)						
G. fuscus sp. nov.	4.5 (4.0–5.2)	1.5 (0.0–3.1)					
G. makira sp. nov.	5.4 (4.6–7.1)	4.5 (3.8–5.6)	0.4 (0.0–1.1)				
G. ampondo sp. nov.	8.2 (7.9–8.3)	8.0 (7.5–8.8)	7.4 (7.0–8.5)	NA			
G. bemiray sp. nov.	8.8 (8.0–10.0)	9.0 (7.7–10.7)	9.5 (8.6–11.1)	8.7 (8.1–9.2)	0.9 (0.0–1.7)		
G. sp. Ca33	6.0 (5.4–6.2)	6.2 (5.4–7.1)	6.7 (6.3–7.3)	8.1 (8.1–8.1)	9.8 (9.5–10.2)	NA	
G. sp. Ca19	9.0 (8.6–9.1)	8.5 (7.3–9.8)	7.8 (7.3–9.6)	4.2 (4.2–4.6)	7.9 (7.5–8.2)	8.1 (8.1–8.1)	0.4 (0.0–1.5)

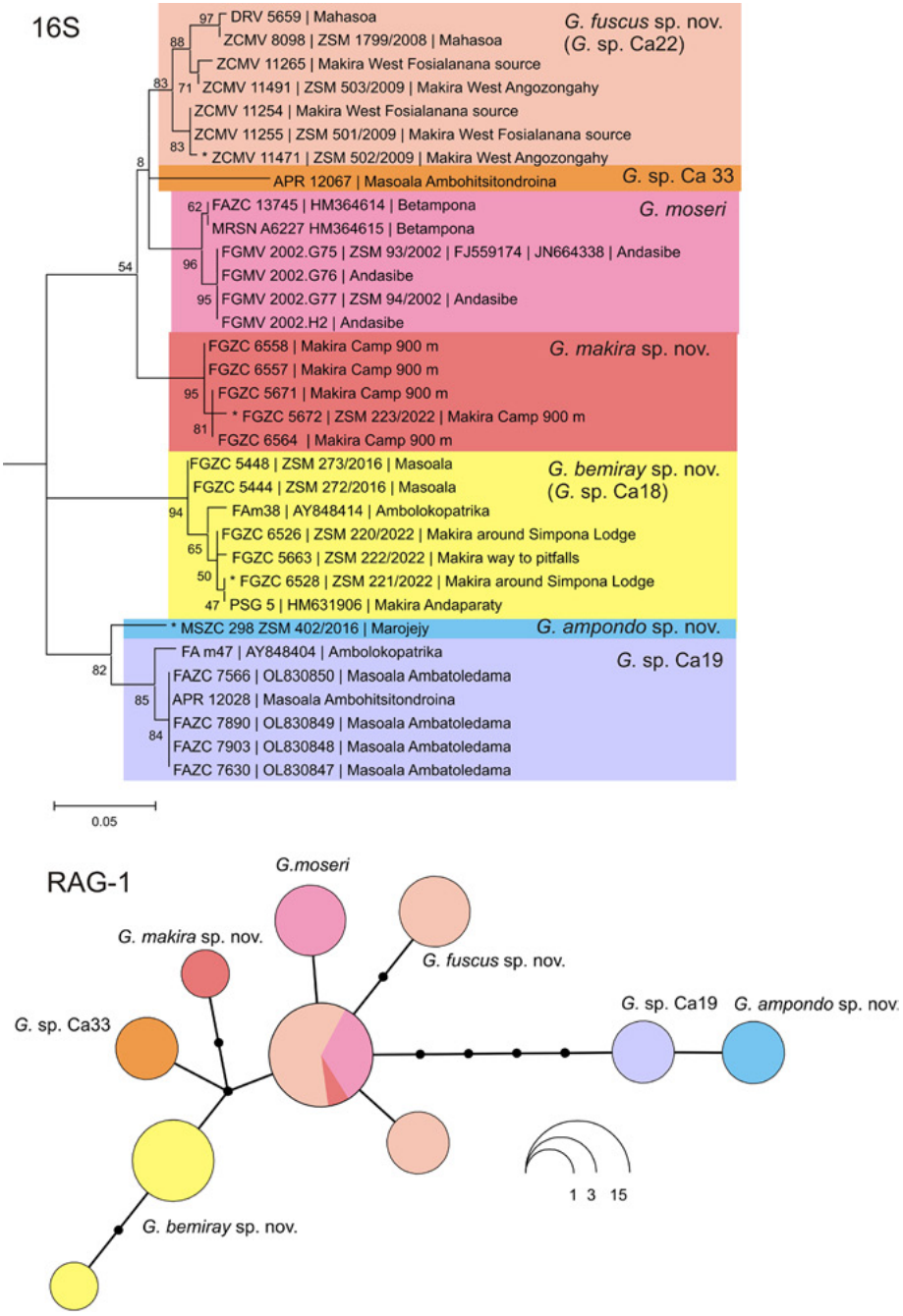

Fig. 1. Maximum-Likelihood phylogenetic tree of the *Gephyromantis moseri* complex calculated from 33 sequences of the mitochondrial 16S rRNA gene (490 bp alignment). Numbers at nodes are bootstrap proportions in percent (500 replicates). The tree was rooted with a sequence of *G. redimitus* (removed graphically for better representation of ingroup relationships). The haplotype network is based on phased RAG-1 sequences (429 bp) of 18 specimens (every specimen thus represented with two sequences in the alignment). Small black dots represent additional mutational steps. Individuals were coloured according to their grouping in mitochondrial lineages. Holotypes in the phylogenetic tree are marked with an asterisk.

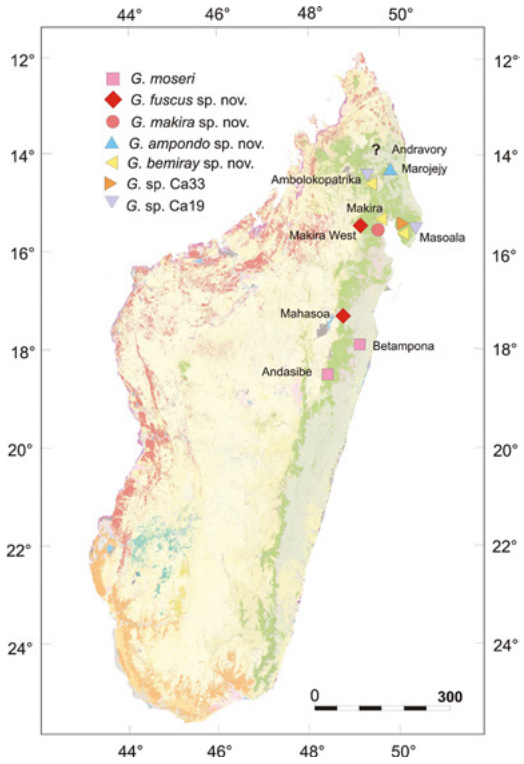

Fig. 2. Map of Madagascar showing distribution records of the *Gephyromantis moseri* complex confirmed by molecular data. Basemap shows vegetation across Madagascar from the Madagascar Vegetation Mapping Project (Moat & Smith 2007; formerly available at www.vegmad.org). Vegetation is coloured as follows: green, humid forest (rainforest); red, western dry deciduous forest; bluish, western subhumid forest; orange, south western dry spiny forest-thicket; yellow, tapia forest. Additional specimens of the *G. moseri* complex from Andravory are available in the ZSM collection but did not reveal any DNA sequences and were therefore not considered in this paper.

The analysis of a fragment of the RAG-1 gene (429 bp for 18 specimens; Fig. 1) resulted in a network of 10 distinct haplotypes, with those of *G. ampondo* sp. nov. and *G.* sp. Ca33 being five mutational steps apart from the others. One haplotype was shared between *G. moseri*, *G. fuscus* sp. nov. and *G. makira* sp. nov. while all other mitochondrial lineages had unique haplotypes only.

Bioacoustics

All known advertisement calls in the *G. moseri* species complex are characterized by being clearly pulsed and repeated in call series (Fig. 3). However, among the calls analysed certain qualitative and quantitative differences are obvious. Compared to calls of nominal *G. moseri* from the type locality Andasibe, calls from Mahasoa and Makira West (*G. fuscus* sp. nov.) differ by being composed of two pulsed notes (versus one), longer call duration (113–147 versus 74–88 ms), and lower dominant frequency (2965–3492 versus 4344–4540 Hz). Calls from Makira (*G. bemiray* sp. nov.) mainly differ from those of *G. moseri* by lower pulse repetition rate within calls (180–190 versus 330 pulses/s) and lower dominant frequency (2939–3384 versus 4344–4540 Hz). Furthermore, calls of *G. bemiray* sp. nov. are unique in the complex being emitted in short call series grouping 2–5 calls only (versus very long call series). In summary, the limited bioacoustic data available for certain phylogenetic clades are in clear support of their evolutionary lineage divergence at the species level, as observed advertisement call differences are beyond those that can be referred to intra-specific call variation (see Köhler et al. 2017).

Morphology

Examination of morphological characters revealed a high similarity among individuals assigned to the various genetic lineages. Several characters showed some variability (Figs 4–8), such as colour pattern, conformation of tubercles and ridges on the dorsum, and relative hindlimb length, but much of this variation was found within rather than among lineages (see Variation section in species accounts below for details). However, some consistent morphological differences among lineages were observed, as summarized in the following: (1) Although body size showed a certain variation within lineages, there were two clear size classes recognizable (Table 2): *G. moseri* and *G. fuscus* sp. nov. were small (male SVL 26.9–31.5 mm) compared to the other lineages (male SVL 30.9–37.1 mm) where *G. bemiray* sp. nov. apparently reaches the largest body sizes. (2) Specimens from the northernmost lineage (*G. ampondo* sp. nov.) from Marojejy had an overall distinctive appearance, although the observed body shape differences are not conclusively reflected in the measurements taken. Differences especially concern the head, which appears stouter, with distinct interocular tubercles, shorter spine-like supraocular tubercles (especially in Marojejy specimens), and a distinctly more concave (rather than straight) canthus rostralis and loreal region. (3) Size of and number of gland granules in femoral (macro) glands (see Glaw et al. 2000, Vences et al. 2007) provide a further character to distinguish some of the species. In *G. moseri* and *G. fuscus* sp. nov., the glands are quite prominent and rather wide, consisting of only about 6–8 large

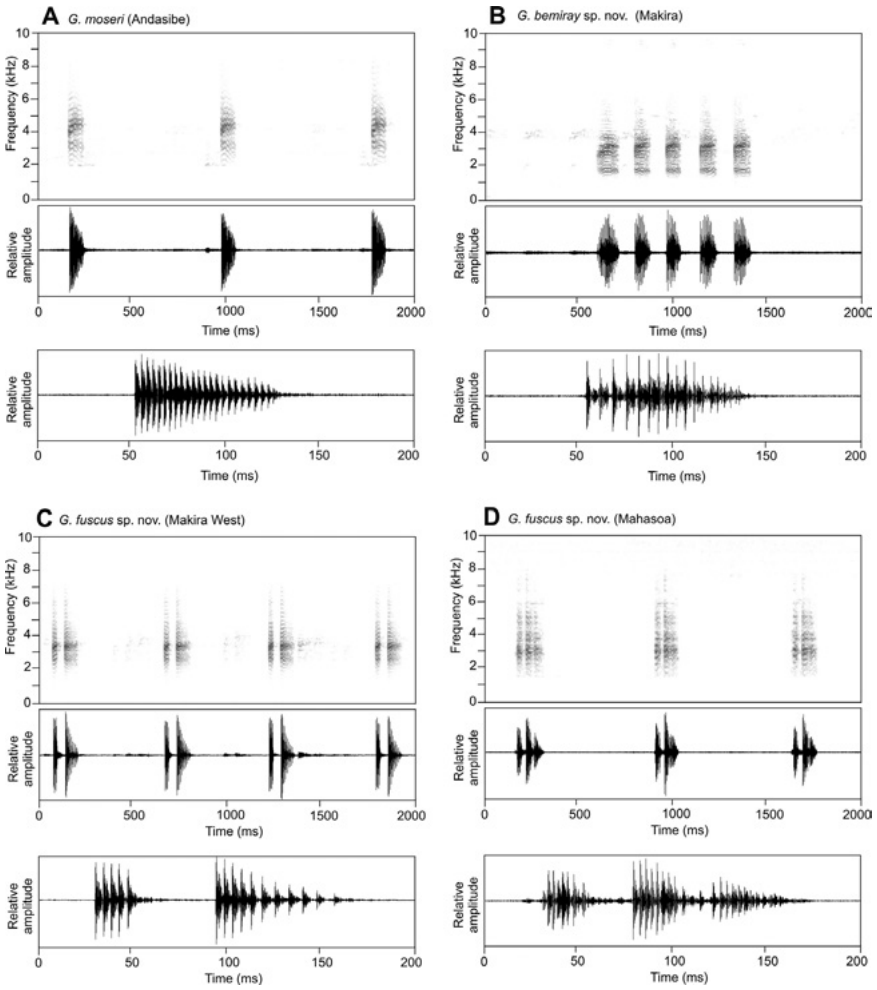

Fig. 3. Audiospectrograms and oscillograms of advertisement calls of: **A.** *Gephyromantis moseri* from Andasibe (high-pass filtered at 2000 Hz); **B.** *G. bemiray* sp. nov. from Makira (high-pass filtered at 500 Hz); **C.** *G. fuscus* sp. nov. from Mahasoa (high-pass filtered at 1500 Hz) and **D.** *G. fuscus* sp. nov. from Makira (western slope).

gland granules, not distinctly pigmented in life. In contrast, in *G. ampondo* sp. nov. and *G. bemiray* sp. nov., the glands are less prominent, consisting of 15–20 gland granules which are yellowish in life in *G. ampondo* sp. nov. Unfortunately, no tadpoles of any lineage of the *G. moseri* complex have so far been collected, and therefore, a comparison of larval morphology is not possible.

Taxonomy

Data assembled in this study clearly demonstrate the existence of multiple species in the *G. moseri* complex. Strongest evidence for this conclusion comes from (1) the substantial differences in advertisement calls among three of the genetic lineages identified (*G. moseri*, *G. fuscus* sp. nov., *G. bemiray* sp. nov.), and (2) the occurrence, on the eastern slope of the Makira Reserve, of two genetic lineages (*G. makira* sp. nov. and *G. bemiray* sp. nov.), in close geographic proximity but without genetic admixture in the mitochondrial and nuclear markers studied (although the latter line of evidence is less robust due to relatively low sample sizes especially for RAG-1). In addition, morphological differences were found to distinguish several of the lineages, with *G. ampondo* sp. nov. being distinct from all other lineages by its head shape and distinct interocular tubercles. In summary,

the majority of lineages can be distinguished from each other either by concordant differentiation in mitochondrial and nuclear genes, morphology, or bioacoustics and several by all of these lines of evidence. For one lineage, herein described as *G. makira* sp. nov., no bioacoustic data are available and no conclusive morphological differences to *G. moseri* and *G. fuscus* sp. nov. were found; however, its high 16S divergence to these lineages (with a minimum distance of 3.8 %) and the fact that it cannot be phylogenetically assigned to either of them makes a status of distinct species most likely.

In conclusion, the available evidence suggests that all of the major lineages in the *G. moseri* complex most probably represent distinct species under both evolutionary and biological species criteria. However, for two lineages, *G.* sp. Ca19 and Ca33, data are extremely fragmentary: *G.* sp. Ca33 is known from only a single specimen which is distinct in mtDNA and has a unique RAG-1 haplotype, but the voucher was not available for examination; *G.* sp. Ca19 is defined as distinct by mitochondrial and nuclear DNA (the latter from only one specimen), but again, voucher specimens were not available for examination. An in-depth taxonomic analysis of *G.* spp. Ca19 and Ca33 is thus postponed to future studies. Here, in the following accounts, we provide formal descriptions of the other four deep lineages that, besides *G. moseri*, make up this species complex.

Table 2. Morphometric measurements (all in mm) of specimens of the *Gephyromantis moseri* complex. For abbreviations of measurements, see Materials and methods; other abbreviations: HT, holotype; PT, paratype; M, male; F, female; NM, not measured; NA, not applicable. Asterisks (*) mark specimens that were not genotyped and that are assigned to lineages based only on their geographical provenance.

Catalogue number	Field number	Locality	Sex	Status	SVL	HW	HL	TD	ED	END	NSD
G. moseri											
ZSM 935/2000 *	NA	Andasibe	M	HT	28.6	9.5	11.4	1.7	3.7	2.9	1.6
ZFMK 60025 *	NA	Andasibe	M	PT	30.1	9.9	11.9	1.9	3.5	3.3	1.6
ZFMK 60026 *	NA	Andasibe	M	PT	26.9	9.5	10.7	1.8	3.5	2.9	1.7
ZSM 93/2002	FGMV 2001.1295	Andasibe	F	–	32.8	11.0	13.2	1.9	5.0	3.8	1.9
ZSM 94/2002	FGMV 2001.1297	Andasibe	J	–	20.5	NM	NM	NM	NM	NM	NM
G. fuscus sp. nov.											
ZSM 502/2009	ZCMV 11471	Makira West	M	HT	29.8	10.2	11.6	1.7	4.0	3.3	1.7
ZSM 503/2009	ZCMV 14491	Makira West	M	PT	29.8	10.0	11.6	2.2	4.2	3.2	1.7
ZSM 501/2009	ZCMV 11255	Makira West	M	PT	28.3	10.0	11.7	2.2	4.2	3.7	1.6
ZSM 1799/2008	ZCMV 8098	Mahasoa	M	PT	30.5	10.1	12.0	2.4	4.6	3.6	2.2
ZSM 1801/2008	ZCMV 8099	Mahasoa	M	PT	28.4	9.5	11.4	2.7	4.0	3.6	2.0
G. makira sp. nov.											
ZSM 223/2022	FGZC 5672	Makira 900 m	F	HT	32.5	11.3	13.0	1.9	4.6	4.0	2.0
G. bemiray sp. nov.											
ZSM 221/2022	FGZC 6528	Makira East	M	HT	34.5	12.5	14.3	2.5	5.3	4.0	2.6
ZSM 220/2022	FGZC 6526	Makira East	M	PT	32.5	11.0	13.1	2.0	5.2	3.5	2.1
ZSM 273/2016	FGZC 5448	Masoala	M	PT	37.1	13.2	14.9	2.4	5.6	4.5	2.0
MRSN-A 4033 *	FAZC 7040	Ambolokopatrika	M	PT	35.1	11.4	13.3	2.0	4.4	3.7	2.1
MRSN-A 4036 *	FAZC 7010	Ambolokopatrika	M	PT	34.9	12.2	13.5	2.4	4.6	3.7	1.7
MRSN-A 4032 *	FAZC 7011	Ambolokopatrika	M	PT	34.3	11.0	12.8	2.0	4.2	3.6	1.9
MRSN-A 4042 *	FAZC 7370	Ambolokopatrika	M	PT	30.9	10.5	12.1	1.9	4.4	3.0	1.9
MRSN-A 4034	FAZC 7009	Ambolokopatrika	M	PT	35.5	11.8	13.7	2.1	4.5	4.0	2.0
MRSN-A 4037 *	FAZC 7349	Ambolokopatrika	M	PT	30.7	10.2	11.3	2.0	3.9	3.2	1.7
ZSM 222/2022	FGZC 5663	Makira East	F	PT	33.5	11.3	13.4	2.5	5.2	4.0	2.1
ZSM 272/2016	FGZC 5444	Masoala	F	PT	39.4	13.2	15.9	3.0	5.0	4.7	2.1
MRSN-A 4031 *	FAZC 6786	Ambolokopatrika	F	PT	36.7	11.4	13.9	2.1	4.1	3.9	1.9
G. ampondo sp. nov.											
ZSM 402/2016	MSZC 298	Marojejy	M	HT	31.7	11.2	13.5	2.4	5.3	3.8	1.8
KU 347344	CRH 1558	Marojejy	M	PT	29.0	10.7	11.9	2.2	4.6	3.6	1.8
ZFMK 59896 *	NA	Marojejy	M	PT	31.5	11.3	12.6	1.8	4.1	3.3	1.4

Continued on next page.

Gephyromantis moseri (Glaw & Vences, 2002)

Fig. 4

Holotype. ZSM 935/2000 (originally ZFMK 60024), adult male, collected by F. Glaw and N. Rabibisoa on 18 December 1994 at Andasibe (approximate coordinates: 18.9229° S, 48.4186° E, ca. 850–900 m above sea level), eastern Madagascar.

Paratypes. ZFMK 60025–60026, two adult males, same locality and collecting dates as holotype.

Diagnosis. Within the subgenus *Duboimantis*, *G. moseri* can be recognized by combination of moderate body size (SVL 28.6–32.8 mm), males with a greyish, largely distensible and slightly bilobed subgular vocal sac and with well-defined femoral glands, horizontal tympanum diameter about half of eye diameter, lateral metatarsalia largely separated, and dorsal surface with large granules and dermal spines, including one conspicuous large spine above each eye and dorsolateral ridges discontinuous and forming a chevron-like pattern on the dorsum. For distinction of other species of the *G. moseri* complex described herein, see diagnoses in the respective species accounts below.

NND	HAL	FORL	HIL	FOTL	FOL	TIBL	FGL	FGW
2.5	9.5	20.8	54.0	23.9	16.3	NM	4.1	1.7
2.4	10.3	21.4	57.4	25.2	16.7	NM	4.5	1.8
2.4	9.0	19.0	53.3	22.5	14.5	NM	4.6	2.0
2.9	11.1	21.7	65.0	28.0	18.7	20.8	NA	NA
NM	NM	NM	NM	NM	NM	NM	NA	NA
2.9	9.1	19.1	53.3	23.2	15.5	16.8	4.2	2.0
2.8	10.2	20.9	56.2	24.3	16.5	18.0	3.9	2.0
2.8	9.8	19.0	54.7	24.4	16.0	17.5	3.7	2.0
2.6	10.3	20.0	55.9	25.4	17.0	18.2	4.8	2.6
2.7	10.0	21.0	56.9	25.2	18.0	18.6	3.7	2.2
3.2	10.0	20.5	65.0	28.8	18.0	21.6	NA	NA
3.1	11.0	21.5	64.0	28.0	18.6	19.9	4.9	1.8
2.7	10.9	22.3	60.0	27.0	17.5	19.3	4.6	1.5
3.1	10.6	22.0	58.8	25.4	17.1	18.8	3.3	1.5
2.8	10.0	21.3	57.1	24.5	16.6	NM	4.7	2.4
2.8	10.1	21.8	59.3	25.6	17.0	NM	4.3	1.5
2.8	10.0	21.4	59.6	26.0	17.2	NM	5.0	1.9
2.8	9.2	19.2	51.8	22.7	14.9	NM	4.6	2.1
2.8	10.1	21.3	58.8	26.2	17.1	NM	5.0	1.9
2.7	9.9	20.0	52.5	24.2	16.3	NM	3.9	2.0
2.8	11.0	21.9	68.1	29.8	19.6	22.6	NA	NA
2.9	11.0	24.6	68.5	30.3	20.2	22.4	NA	NA
2.9	10.9	23.5	65.9	28.6	18.6	NM	NA	NA
2.8	10.0	19.8	55.4	23.9	16.3	17.4	5.7	1.9
2.8	9.4	19.9	55.7	23.9	15.9	18.1	4.5	1.8
2.5	10.7	22.4	60.1	26.3	18.4	NM	3.5	1.2

Continued from last page.

Natural history. As reported by Glaw & Vences (2002), calling specimens were perched 0.5–1.5 m high in the vegetation along a small brook in primary rain forest, and calling took place immediately after dusk, stopping around 21:00 h. New specimens collected for this study were found during the day, in the leaf litter around a small seepage-like stream in rainforest.

Advertisement calls. Calls recorded at the type locality Andasibe on 18 December 1994, 19:20 h (air temperature 20 °C; Vences et al. 2006, CD 2, track 7), consist of a single pulsed note, repeated in long call series at somewhat irregular intervals. Pulses within calls are barely fused and clearly separated. Slight overall amplitude modulation is evident in each call, with maximum call energy being present at the beginning of the call, constantly decreasing towards its end. Numerical parameters of 14 analysed calls of one individual are as follows: call duration (= note duration) 74–88 ms (81.4 ± 3.6 ms); inter-call interval within call series 634–1789 ms (1033.0 ± 384.3 ms); pulses/call 23–30 (26.6 ± 1.7); pulse repetition rate within calls approximately 330 pulses/s; dominant frequency 4344–4540 Hz (4451 ± 64 Hz); prevalent bandwidth 2500–5800 Hz.

Distribution. *G. moseri* is known from (1) the type locality, Andasibe, and (2) according to mitochondrial DNA sequences from Rosa et al. (2012), from Betampona (Sahabefoza). The elevational range occupied by the species is between ca. 350 m (Sahabefoza) and 900 m (Andasibe).

Gephyromantis fuscus sp. nov.

Figs 5, 9

Remark. This species has previously been considered as *G.* sp. 22 by Vieites et al. (2009) and Kaffenberger et al. (2012), and as *G.* sp. Ca22 by Perl et al. (2014).

Holotype. ZSM 502/2009 (ZCMV 11471), adult male, collected on 21 June 2009 by M. Vences, D. R. Vieites, F. M. Ratsoavina, R. D. Randrianiaina, E. Rajeriarison, T. Rajoafiarison, J. L. Patton, and C. Patton, at Angozongahy campsite, western side of Makira Reserve (15.4370° S, 49.1186° E, 1009 m above sea level), northeastern Madagascar.

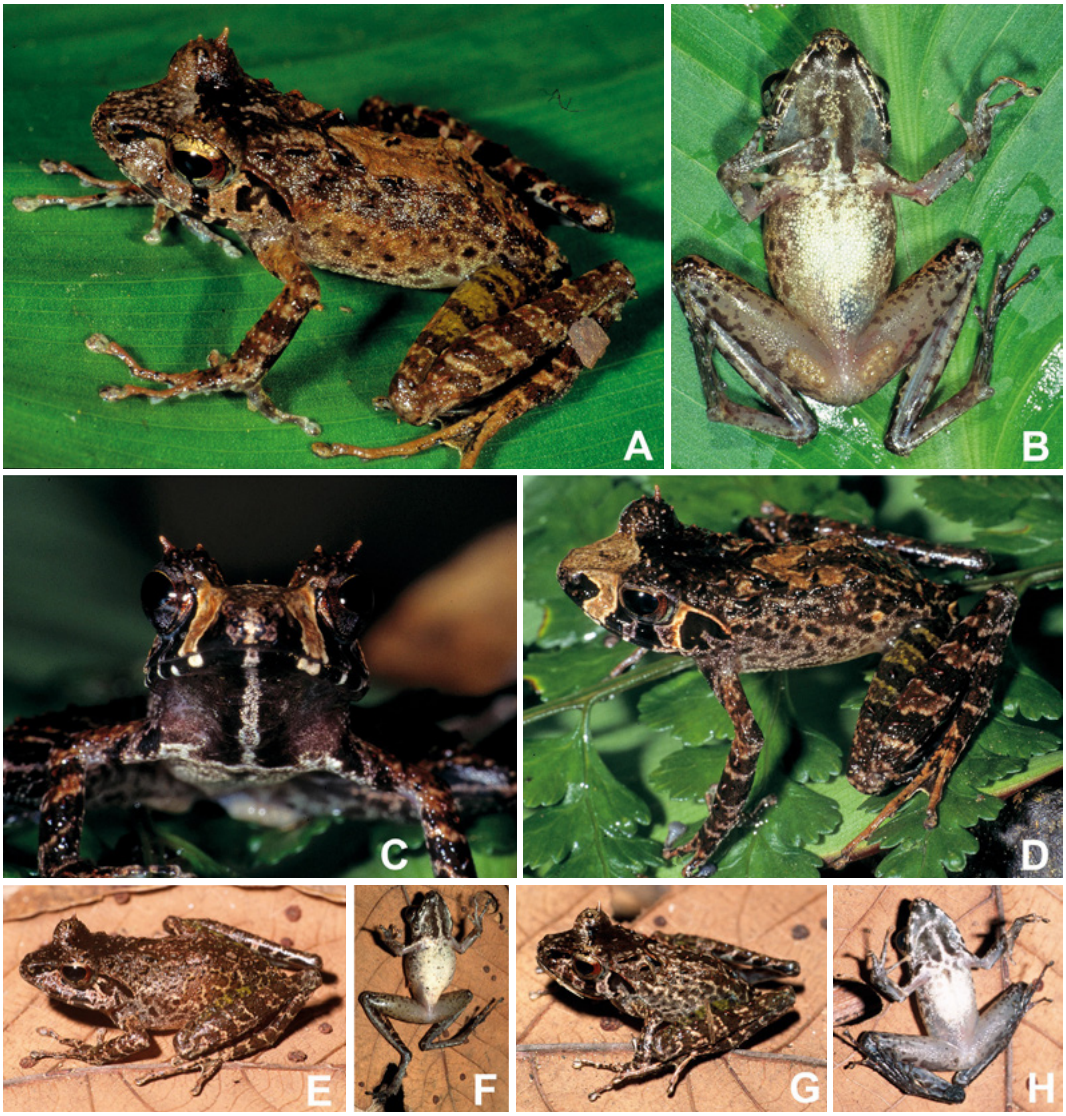

Fig. 4. *Gephyromantis moseri* from Andasibe in life. **A–B.** Male holotype ZSM 935/2000 in dorsolateral and ventral views, photographed 1994; **C–D.** additional specimen from Andasibe (not reliably assignable to a voucher specimen) photographed 1994, in frontal and dorsolateral views; **E–F.** female ZSM 93/2002 (FGMV 2001.1295) in dorsolateral and ventral views; **G–H**. subadult ZSM 94/2002 (FGMV 2001.1297) in dorsolateral and ventral views.

Paratypes. Six specimens from northeastern Madagascar: ZSM 503/2009 (ZCMV 11491), adult male, with same collection data as holotype; ZSM 501/2009 (ZCMV 11255), adult male, UADBA-ZCMV 11254 (sex unknown, not studied morphologically) and UADBA-ZCMV 11265 (sex unknown, not studied morphologically), all three collected on 23–24 June 2009 by M. Vences, D. R. Vieites, F. M. Ratsoavina, R. D. Randrianiaina, E. Rajeriarison, T. Rajoafiarison, J. L. Patton, and C. Patton, at the source of the Fotsialanana river, western side of the Makira Reserve (15.4668° S, 49.1289° E, 1067 m a. s. l.); ZSM 1799/2008 (ZCMV 8098) and ZSM 1801/2008 (ZCMV 8099), two adult males, collected on 14 February 2008 by D. R. Vieites, J. L. Patton, C. Patton, P. Bora, and M. Vences, at Mahasoa forest near Ambodisakoa village (17.2977° S, 48.7020° E, 1032 m a. s. l.).

Diagnosis. Assigned to the *Gephyromantis moseri* complex in the subgenus *Duboimantis* based on (1) lack of nuptial pads in males, (2) presence of

Fig. 5. *Gephyromantis fuscus* sp. nov. in life. **A–B.** Male paratype ZSM 1799/2008 (ZCMV 8098) from Mahasoa Forest in dorsolateral and ventral views; **C–D.** male holotype ZSM 502/2009 (ZCMV 11471) from Angozongahy Campsite, western slope of Makira, in dorsolateral and ventral views.

type 2 femoral glands (Glaw et al. 2000) in males, (3) moderately enlarged tips of fingers and toes, (4) lateral metatarsalia separated by webbing, (5) presence of foot webbing, (6) absence of a distinct white spot in the center of the tympanum, (7) presence of partial, discontinuous dorsolateral ridges, (8) presence of supraocular spines, (9) medium body size (28–31 mm SVL), (10) tympanum higher than wide and about half as wide as eye, (11) weakly expressed or absent interocular tubercles, and (12) molecular phylogenetic relationships. Within the *G. moseri* complex, distinguished from *G. moseri* by advertisement call structure (two vs. one notes per call, call duration 113–147 vs. 74–88 ms, dominant frequency 2965–3492 vs. 4344–4540 Hz), and in most specimens, by a different pattern of inner dorsolateral ridges which are centrally interrupted and convex (vs. anteriorly connected or almost connected, and forming a chevron). The new species is also characterized by numerous diagnostic nucleotide positions in the mitochondrial 16S rRNA gene: MolD identified a robust diagnostic nucleotide combination of "T" at site 211, "A" at site 258, "G" at site 388 (positions relative to the full 16S rRNA gene of *Mantella madagascariensis*). For distinction from other new species of the *G. moseri* complex described herein, see Diagnoses in the respective species accounts below.

Description of holotype. Specimen in excellent state of preservation, with muscle and skin tissue removed from right thigh for molecular analysis, and skin surrounding left femoral gland partly

detached for gland examination (Fig. 9). Snout–vent length 29.8 mm. For other measurements see Table 2. Body slender; head longer than wide, wider than body; snout rounded in dorsal view, truncate in lateral view; nostrils directed laterally, protuberant, much nearer to tip of snout than to eye; canthus rostralis distinct, weakly concave; loreal region weakly concave; tympanum distinct, ovoid, higher than wide, its horizontal diameter 43 % of eye diameter; supratympanic fold distinct, straight; tongue ovoid, distinctly bifid posteriorly; vomerine teeth distinct, in two small rounded aggregations, positioned posteromedial to choanae; choanae rounded; maxillary teeth present. Weakly distinguishable, small, slightly dark dermal fold (indicating inflatable skin of the vocal sac) posterolaterally on throat next to posterior ends of lower jaws. Arms slender, subarticular tubercles single; inner metacarpal tubercle and two (partly fused) outer metacarpal tubercles relatively well developed; fingers without webbing; relative length of fingers 1 < 2 < 4 < 3, second finger distinctly shorter than fourth; finger discs distinctly enlarged, nuptial pads absent. Hindlimbs slender; tibiotarsal articulation reaching distinctly beyond snout tip when hindlimb is adpressed along body; lateral metatarsals separated by webbing; inner metatarsal tubercle distinct, outer metatarsal tubercle small but recognizable; webbing formula of foot 1 (1.5), 2i (1.5), 2e (1), 3i (2), 3e (1.25), 4i (2.5), 4e (2.25), 5 (1); relative toe length 1 < 2 < 3 < 5 < 4; fifth toe clearly longer than third toe; toe discs distinctly enlarged. Skin dorsally rather smooth with some granules laterally and a distinct network of prominent ridges: inner dorsolateral ridge (as defined in Vences & Glaw 2001) present only in the area of the forelimb insertion, forming a centrally interrupted convex pattern. Outer dorsolateral ridges present between eyes and forelimb insertion in the form of several ridge-like tubercles. Small but clearly recognizable supraocular tubercles present. Interocular tubercles were recognizable in life relatively small and weakly expressed (Fig. 5). Ventral skin smooth on throat, chest and limbs, slightly granular on posterior portion of abdomen. Femoral macroglands of type 2 (sensu Glaw et al. 2000) well delimited externally, consisting of about 6 separate gland granules on the left side.

After 14 years of preservation in ethanol, dorsally brown with some irregular and poorly defined lighter and darker markings. The dorsolateral ridges are lined by sharply delimited dark brown colour. A dark brown bar runs between the eyes, and anterior to this bar, the colour on the dorsal surface of the head is light-brown to beige. A dark brown stripe runs directly underneath the canthus rostralis and ventrally of the supratympanic ridge. Tympanum is dark brown. Two dark brown patches on the lower lip which continue onto the lower lip and here are delimited by whitish colour; especially distinct in a patch underneath the eye. Hindlimbs with about four relatively well delimited dark brown crossbands both on shank and thigh, upper arm with three dark crossbands. Ventrally cream, with brown mottling on limbs and chest, and dense brown pigmentation on throat; a medial light stripe is distinct and well delimited in the chest region and anteriorly becomes less distinct on the throat.

Etymology. The species name is a Latin adjective, "fuscus" meaning "brown", making reference to the inconspicuous brown colour of this species.

Variation. Measurements of 4 paratypes (all males) are included in Table 2. Their SVL ranges from 28.4–30.5 mm. Females of this species are unknown. No obvious differences in body size or other morphological characters are apparent between specimens from Mahasoa and Makira. Femoral glands are prominent in all specimens, but with some differences in size; e. g., in Mahasoa, ZSM 1799/2008 has clearly larger glands than ZSM 1801/2008. The inner dorsolateral ridges can be more chevron-like (e. g., ZSM 1801/2008) or forming two convex ridges (ZSM 1799/2008), or forming two small ridges with a medial tubercle, but they are not in anterior contact with each other (forming a closed chevron) in any individual. The ground colour laterally on the head is cream to light brown in all specimens, interrupted by brown vertical bars and blotches. None of the specimens has a colour pattern conspicuously deviating from that of the holotype.

Natural history. At Makira and Mahasoa, males were found calling at night, perched in the low vegetation (at 1 m or less above the ground), in intact (Makira) or degraded (Mahasoa) rainforest, close to streams.

Advertisement calls. Advertisement calls recorded at Mahasoa on 14 February 2008, 22:30 h (air temperature not recorded but estimated ca. 20 °C) consist of two short, pulsed notes repeated in rapid succession, with the first note being distinctly shorter compared to the second note of the call. In many cases, the second note of the call shows some further division in two more or less distinctly separated pulse groups. However, in some calls this subdivision of the second note is absent. Maximum call energy is present at the beginning of each note, with the second note of each call exhibiting slightly higher maximum energy when compared to the first note. Calls are repeated in long series at somewhat irregular intervals. Numerical parameters of 17 analysed call of one individual are as follows:

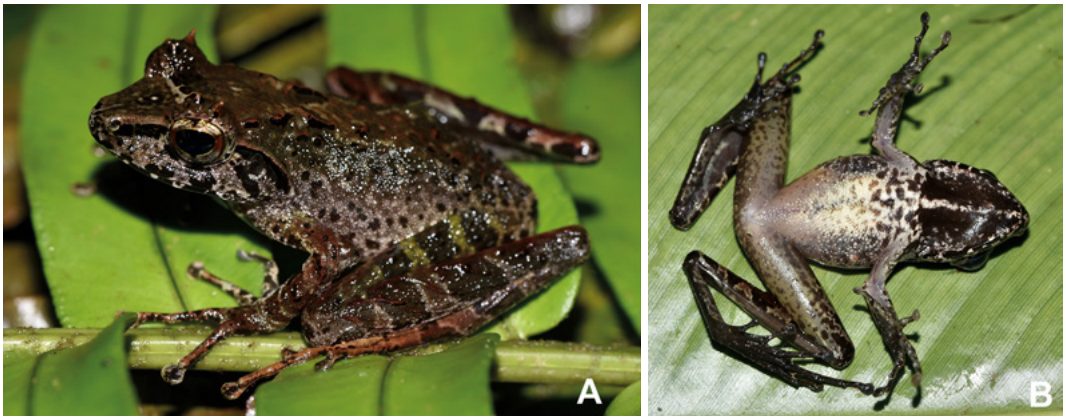

Fig. 6. Female holotype of *Gephyromantis makira* sp. nov., ZSM 223/2022 (FGZC 5672) in life, in dorsolateral and ventral views.

call duration 113–144 ms (129.4 ± 9.4 ms); duration 1st note 24–35 ms (28.4 ± 3.3 ms); duration 2nd note 65–91 ms (77.5 ± 8.2 ms); inter-note interval within calls 13–25 ms (19.7 ± 3.2 ms); pulses/1st note 6–11 (8.7 ± 1.8); pulses/2nd note 18–23 (20.3 ± 1.7); pulse repetition rate within notes varied approximately between 270–400 pulses/s; inter-call interval within call series 585–1635 ms (936.3 ± 358.4 ms); dominant frequency 2965–3170 Hz (3023 ± 75 Hz); prevalent bandwidth 1500–6500 Hz.

Advertisement calls recorded on 21 June 2009, 17:30 h, at Angozongahy campsite, western side of Makira Reserve (air temperature not recorded but estimated ca. 20 °C) agree in general character with those from Mahasoa in consisting of two pulsed notes and calls being repeated in long call series. However, the calls from Makira West differ from those of Mahasoa by the lack of any further subdivision of the calls' second note, slightly longer inter-note intervals within calls, lower number of pulses per note and thus lower pulse rate within notes. Numerical parameters of 65 analysed call of one individual (call voucher ZCMV 11471) are as follows: call duration 122–147 ms (135.0 ± 6.8 ms); duration 1st note 20–32 ms (25.5 ± 3.7 ms); duration 2nd note 64–81 ms (73.5 ± 5.1 ms); inter-note interval within calls 31–42 ms (35.7 ± 3.1 ms); pulses/1st note 4–6 (5.1 ± 0.5); pulses/2nd note 10–14 (12.4 ± 1.2); pulse repetition rate within notes varied approximately between 150–270 pulses/s; inter-call interval within call series 320–1801 ms (678.3 ± 287.7 ms); dominant frequency 3267–3492 Hz (3402 ± 81 Hz); prevalent bandwidth 1500–6800 Hz.

Distribution. The new species is known from two localities, (1) the western slope of the Makira Reserve (here at two sites: the type locality Angozongahy campsite and the source of the Fotsialanana River), and (2) Mahasoa Forest. The species is known from elevations of 1009–1067 m a. s. l.

Gephyromantis makira sp. nov.

Figs 6, 9

Holotype. ZSM 223/2022 (FGZC 5672), adult female, collected on 22 March 2022 by J. M. Rafanoharana, H. Raherinjatovo, and F. Glaw, at the Makira Reserve, "Camp 900 m" (15.1780° S, 49.6244° E, 891 m a. s. l.), northeastern Madagascar.

Paratypes. UADBA-FGZC 5671, female, same data as holotype; UADBA-FGZC 6557 (male) and UADBA-FGZC 6558 (male), both collected on 17 April 2022 by J. M. Rafanoharana and H. Raherinjatovo at the same locality as holotype; UADBA-FGZC 6564 (female), collected on 19 April 2022 by J. M. Rafanoharana and H. Raherinjatovo at the same locality as holotype. The four topotypic paratypes were not studied morphologically, but unambiguously assigned to *G. makira* based on their position in the mitochondrial tree (Fig. 1).

Diagnosis. Assigned to the *Gephyromantis moseri* complex in the subgenus *Duboimantis* based on (1) moderately enlarged tips of fingers and toes, (2) lateral metatarsalia separated by webbing, (3) presence of foot webbing, (4) absence of a distinct white spot in the center of the tympanum, (5) presence of partial, discontinuous dorsolateral ridges, (6) presence of supraocular spines, (7) medium body size (33 mm SVL), (8) tympanum higher than wide and about half as wide as eye, and (9) molecular phylogenetic relationships. Within the *G. moseri* complex, weakly distinguished from *G. moseri* and *G. fuscus* by inner dorsolateral ridges

forming a relatively indistinct half-circle interrupted anteromedially (vs. anteromedially closed chevron in *G. moseri*, and forming a more convex pattern with a generally wider anteromedial gap in *G. fuscus*). It is also characterized by numerous diagnostic nucleotide positions in the mitochondrial 16S rRNA gene: MolD identified a robust diagnostic nucleotide combination of "A" at site 46, "G" at site 214, "C" at site 412 (positions relative to the full 16S rRNA gene of *Mantella madagascariensis*). For distinction from other new species of the *G. moseri* complex described herein, see Diagnoses in the respective species accounts below.

Description of holotype. Specimen in excellent state of preservation, with muscle and skin tissue removed from right thigh for molecular analysis (Fig. 9). Tongue removed. Snout–vent length 32.5 mm. For other measurements see Table 2. Body slender; head longer than wide, slightly wider than body; snout rounded in dorsal and lateral views; nostrils directed laterally, slightly protuberant, much nearer to tip of snout than to eye; canthus rostralis distinct, straight; loreal region weakly concave; tympanum distinct, ovoid, higher than wide, its horizontal diameter 41 % of eye diameter; supratympanic fold distinct, almost straight; tongue ovoid removed; vomerine teeth distinct, in two small rounded aggregations, positioned posteromedial to choanae; choanae rounded; maxillary teeth present. Arms slender, subarticular tubercles single; inner metacarpal tubercle and two (partly fused) outer metacarpal tubercles present but rather indistinct, possibly due to state of fixation; fingers without webbing; relative length of fingers 1<2<4<3, second finger distinctly shorter than fourth; finger discs distinctly enlarged. Hindlimbs slender; tibiotarsal articulation reaching far beyond snout tip when hindlimb is adpressed along body; lateral metatarsals separated by webbing; inner metatarsal tubercle distinct, outer metatarsal tubercle small but recognizable; webbing formula of foot 1(1.5), 2i(1.5), 2e(1), 3i(2.25), 3e(1.25), 4i(2.75), 4e(2.5), 5(1); relative toe length 1<2<3<5<4; fifth toe slightly longer than third toe; toe discs distinctly enlarged. Skin dorsally rather smooth with some granules laterally and a network of prominent ridges that are indistinct, probably due to fixation. Inner dorsolateral ridge (as defined in Vences & Glaw 2001) present only in the area of the forelimb insertion, forming a centrally interrupted convex pattern. Outer dorsolateral ridges present between eyes and forelimb insertion in the form of several ridge-like tubercles. Supraocular tubercles poorly recognizable (probably due to fixation but were probably present). Ventral skin smooth on throat, chest and limbs, slightly granular on posterior portion of venter. After two years of preservation in ethanol, dorsally brown with irregular and poorly defined lighter and darker markings. The dorsolateral ridges are lined by sharply delimited dark brown colour. An irregular dark brown bar runs between the eyes, delimited anteriorly by light colour. Head is laterally largely dark brown, including the tympanum, with light markings on upper and lower lips delimiting what in other specimens of the *G. moseri* complex are dark markings. Flanks fading from light brown dorsal to cream-yellowish ventral colour, with rather distinct brown spotting. Hindlimbs with about four relatively well delimited dark brown crossbands on thigh, also present but poorly contrasted on the overall darker shanks. Ventrally cream on chest and yellowish-cream on belly and hindlimbs, with brown mottling being dense on limbs and chest and sparse on belly. Throat almost uniformly dark brown with a thin medial light line.

Etymology. The species name is derived from the Makira Reserve, the only known locality of this species so far. It is used as a noun in apposition.

Variation. Only the holotype was studied morphologically, so data on morphological variation are not available at present.

Natural history. The holotype and one of the paratypes (UADBA-FGZC 5671) were collected on a rainy night perched on a leaf, ca. 1 m above the ground, in rainforest.

Distribution. The species is only known from the type locality on eastern slope of the Makira Reserve, at a local campsite named "Camp 900 m".

Gephyromantis bemiray sp. nov.

Figs 7, 9

Remark. This species has previously been considered as *G.* sp. 18 by Vieites et al. (2009).

Holotype. ZSM 221/2022 (FGZC 6528), collected on 24 March 2022 by J. M. Rafanoharana, H. Raherinjatovo, and F. Glaw, at the Makira Reserve, around Simpona Lodge (15.1992° S, 49.6208° E, 410 m a.s.l.), northeastern Madagascar.

Paratypes. Eleven specimens from northeastern Madagascar: ZSM 220/2022 (FGZC 6526), with same collection data as holotype; ZSM 222/2022 (FGZC 5663), collected on 21 March 2022 by J. M. Rafanoharana, H. Raherinjatovo, and F. Glaw, in the Makira Reserve, close to Simpona Lodge (close to 15.1992° S, 49.6208° E, 410 m a.s.l.); ZSM 272/2016 (FGZC 5444), female, and ZSM 273/2016 (FGZC 5448), adult male, collected on 13 August 2016 by F. Glaw, D. Prötzel, J. Forster, K.

Fig. 7. *Gephyromantis bemiray* sp. nov. in life, in frontal, dorsolateral and ventral views: **A.** Male holotype ZSM 221/2022 (FGZC 6528) with inflated vocal sac emitting advertisement call (image taken from video); **B–D.** male paratype ZSM 220/2022 (FGZC 6526); **E–F.** male paratype ZSM 222/2022 (FGZC 5663).

Glaw, and T. Glaw in Masoala, close to "Eco-Lodge chez Arol" (15.7122° S, 49.9640° E, 21 m a.s.l.); MRSN A4031 (FAZC 6786), female collected on 30 December 1997 by F. Andreone, G. Aprea and J. E. Randrianirina at Ambolokopatrika, Andranomadio Campsite (14.540° S, 49.438° E, 860 m a.s.l.); MRSN A4032 (FAZC 7011), A4034 (FAZC 7009), and A4036 (FAZC 7010), males, all collected at Andranomadio Campsite (data as before excepting for the collecting date, 2 December 1997); MRSN A4033 (FAZC 7040), male collected at Andranomadio Campsite (data as before excepting for the collecting date, 3 December 1997); MRSN A4037 (FAZC 7349) and A4042 (FAZC 7370), males, both collected on 16 and 17 December 1997 by F. Andreone, G. Aprea, and J. E. Randrianirina at Ambolokopatrika, Antsinjorano Campsite (14.543° S, 49.430° E, about 950 m a.s.l.).

Diagnosis. Assigned to the *Gephyromantis moseri* complex in the subgenus *Duboimantis* based on (1) lack of nuptial pads in males, (2) presence of type 2 femoral glands (Glaw et al. 2000) in males, (3) moderately enlarged tips of fingers and toes, (4) lateral metatarsalia separated by webbing, (5) presence of foot webbing, (6) absence of a distinct white spot in the center of the tympanum, (7) presence of partial, discontinuous dorsolateral ridges, (8) presence of supraocular spines, (9) medium body size (31–39 mm SVL), (10) tympanum higher than wide and about half as wide as eye, and (11) molecular phylogenetic relationships. Within the *G. moseri* complex, distinguished from *G. moseri* and *G. fuscus* by inner dorsolateral ridges not forming a distinct, regular pattern (vs. anteriorly connected and forming a chevron in *G. moseri* and a centrally interrupted convex pattern in *G. fuscus*), larger body size (male SVL 30.7–37.1 mm vs. 26.9–31.5 mm), femoral glands consisting of >15 small gland granules (vs. <10 large granules), and advertisement calls emitted in short call series of only 2–5 calls (vs. much longer call series). From *G. makira* the new species differs by larger body size (female SVL 33.5–36.7 mm vs. 32.5 mm). The new species is also characterized by numerous diagnostic nucleotide positions in the mitochondrial 16S rRNA gene: MolD identified a robust diagnostic nucleotide combination of "C" at site 39, "T" at site 135, "A" at site 200 (positions relative to the full 16S rRNA gene of *Mantella madagascariensis*). For distinction from the fourth new species of the *G. moseri* complex described herein, see Diagnosis in the respective species account below.

Description of holotype. Specimen in excellent state of preservation, with muscle and skin tissue removed from right thigh for molecular analysis, and skin surrounding left femoral gland partly detached for gland examination (Fig. 9); tongue damaged. Snout–vent length 34.5 mm. For other measurements see Table 2. Body slender; head longer than wide, wider than body; snout rounded in dorsal view, truncate in lateral view; nostrils directed laterally, protuberant, much nearer to tip of snout than to eye; canthus rostralis distinct, almost straight; loreal region concave; tympanum distinct, ovoid, higher than wide, its horizontal diameter 47 % of eye diameter; supratympanic fold distinct, slightly curved; tongue damaged, but detached part indicates it was distinctly bifid posteriorly; vomerine teeth distinct, in two small aggregations, positioned posteromedial to choanae; choanae rounded; maxillary teeth present. Very weakly distinguishable, small, slightly dark dermal fold (indicating inflatable skin of the vocal sac) in the posterolateral corners of the throat. Arms slender, subarticular tubercles single; inner metacarpal tubercle and two (partly fused) outer metacarpal tubercles relatively well developed; fingers without webbing; relative length of fingers 1 < 2 < 4 < 3, second finger distinctly shorter than fourth; finger discs distinctly enlarged, nuptial pads absent. Hindlimbs slender; tibiotarsal articulation reaching distinctly beyond snout tip when hindlimb is adpressed along body; lateral metatarsals separated by webbing; inner metatarsal tubercle distinct, outer metatarsal tubercle small but recognizable; webbing formula of foot 1 (1), 2i (1.5), 2e (1), 3i (1.5), 3e (1), 4i (2.25), 4e (2), 5 (1); relative toe length 1 < 2 < 3 < 5 < 4; fifth toe slightly but distinctly longer than third toe; toe discs distinctly enlarged. Skin dorsally rather smooth with sparse granulation in the central area and a poorly developed, irregular pattern of longitudinal ridges (possibly poorly recognizable due to fixation); small but clearly recognizable supraocular tubercles present. Interocular tubercles not recognizable, but were visible in life, small and indistinct (Fig. 7). Ventral skin smooth on throat, chest, and limbs, slightly granular on posterior portion of abdomen. Femoral macroglands of type 2 (sensu Glaw et al. 2000) well delimited externally, consisting of about 22 small separate gland granules on the right side.

After two years of preservation in ethanol, dorsally dark brown with poorly recognizable pattern. A thin white line between the eyes marks the border between coloration on head and the remaining body. Dark bars on upper and lower lips as well as light delimitation between them recognisable. Dark crossbands on limbs visible but poorly contrasted. Tympanum light with a characteristic pattern of two upper and one lower spots. Flanks dark brown with weakly contrasted cream spotting. Ventrally cream, with sparse brown mottling on limbs, chest, and throat, and a brown light medial line on chest and throat. Colour of holotype in life only known from screenshots of a video taken while calling (Fig. 7A) and apparently in general similar to colour in preservative.

Etymology. The species name is derived from the Malagasy word "bemiray" meaning "patchwork", referring to the different colours making up the pattern of several of the paratype specimens, i. e., the orange flank colour or the cream-reddish colour of the head. The name is used as a noun in apposition.

Variation. Measurements of all 11 paratypes (8 males and 3 females) are included in Table 2. SVL ranges from 32.5–37.1 mm in males and 33.5–39.4 mm in females, suggesting females may reach slightly larger sizes than males. Specimen ZSM 273/2016 from Masoala has a somewhat more marked canthus rostralis, reminiscent of *G. ampondo* sp. nov. (see below). Several specimens have rather conspicuous colour patterns in life, e. g., a pink-cream band from eye to inguinal region, broadening posterior to tympanum to cover the entire flanks, is present in FGZC 5663 and in ZSM 272/2016; such a pattern is also known from several other *Duboimantis* (e. g., Glaw & Vences 2007). In FGZC 6526, the head anterior to the eyes is uniformly cream. Eye colour in life is greyish cream on the upper and lower part of the iris, with red-brown areas laterally.

Natural history. Specimens were heard calling from low perches in the vegetation, partly on dead leaves on the leaf litter, at night close to a stream in rainforest. At Ambohitsitondroina, a specimen (which however may also belong to *G.* sp. Ca33) was collected on a leaf 0.5 m above the forest floor, at 19:00 h, in almost closed canopy humid forest on a slope (750 m a. s. l.).

Advertisement calls. Advertisement calls recorded on video with an iPhone 12 Pro at Makira on 24 March 2022, 20:00 h (air temperature unknown) from various specimens, including the holotype, consist of a single pulsed note, emitted singly, or more often in short call series in rapid succession and regular intervals. Call series contained 2–5 calls. In some series, the initial call consisted of a shorter note of only 20–40 ms duration. Pulses within calls are barely fused and clearly separated. Slight overall amplitude modulation is evident in each call, with maximum call energy being present either in the first third of the call's duration, or in the middle, decreasing towards its end. Numerical parameters of 22 analysed calls of one individual are as follows: call duration (= note duration) 78–117 ms (90.2 ± 10.4 ms); inter-call interval within call series 70–109 ms (90.9 ± 11.2 ms); pulses/call 15–23 (17.2 ± 2.0); pulse repetition rate within calls approximately 180–190 pulses/s; dominant frequency 2939–3384 Hz (3216 ± 112 Hz); prevalent bandwidth 1200–6500 Hz.

Distribution. The species is known from (1) the type locality on the eastern slope of the Makira Reserve, around Simpona Lodge, (2) the Masoala Peninsula, close to "Eco-Lodge chez Arol", (3) Ambohitsitondroina-Masoala, and (4) Ambolokopatrika (formerly generically classified as "*Mantidactylus asper*", see Andreone et al. 2000). The species occupies an elevational range between ca. 20–900 m a. s. l.

Gephyromantis ampondo sp. nov.

Figs 8, 9

Holotype. ZSM 402/2016 (field number MSZC 298), adult male, collected on 25 November 2016 by M. D. Scherz, C. R. Hutter, J. Razafindraibe, and A. Razafimanantsoa, at Marojejy National Park, "Camp 0" (14.4463° S, 49.7852° E, 310 m above sea level), northeastern Madagascar.

Paratypes. Two specimens: ZFMK 59896, adult male, collected by F. Glaw and O. Ramilison on 4 March 1995 on the Marojejy massif, Campsite 1 (approximate coordinates 14.43° S, 49.77° E, ca. 300 m a. s. l.); KU 347344 (CRH 1558), adult male, with same collection data as holotype.

Diagnosis. Assigned to the *Gephyromantis moseri* complex in the subgenus *Duboimantis* based on (1) lack of nuptial pads in males, (2) presence of type 2 femoral glands (Glaw et al. 2000) in males, (3) moderately enlarged tips of fingers and toes, (4) lateral metatarsalia separated by webbing, (5) presence of foot webbing, (6) absence of a distinct white spot in the center of the tympanum, (7) presence of partial, rather discontinuous dorsolateral ridges, (8) presence of supraocular spines, (9) presence of distinct interocular tubercles, (10) medium body size (31–33 mm SVL), (11) tympanum higher than wide and about half as wide as eye, and (12) molecular phylogenetic relationships. Within the *G. moseri* complex, distinguished from all other species (*G. moseri*, *G. fuscus*, *G. makira*, *G. bemiray*) by larger and more pronounced interocular tubercles (vs. small in most others, absent in *G. makira*) and distinctly concave canthus rostralis and loreal region (vs. straight or weakly concave). Furthermore distinguished from *G. moseri* and *G. fuscus* by femoral glands consisting of > 15 small gland granules (vs. < 10 large granules). The new species is also characterized by numerous diagnostic nucleotide positions in the mitochondrial 16S rRNA gene: MolD identified a robust diagnostic nucleotide combination of "C" at site 112, "T" at site 185, "G" at site 311 (positions relative to the full 16S rRNA gene of *Mantella madagascariensis*).

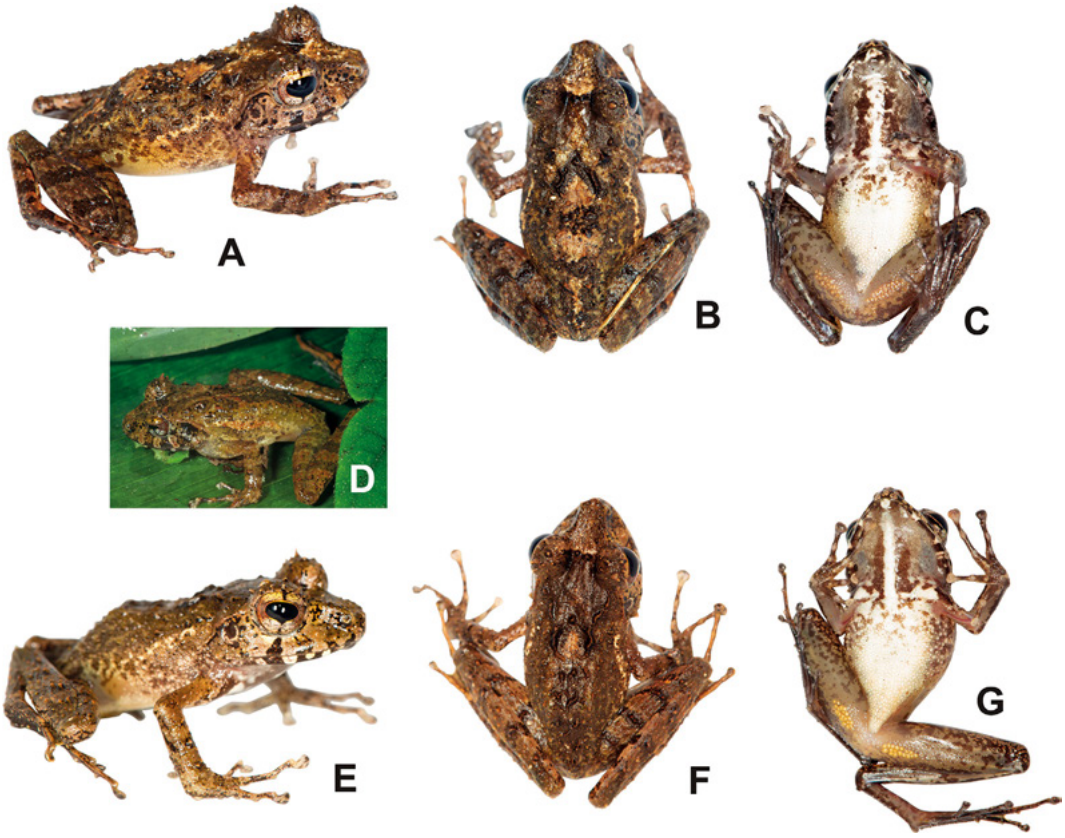

Fig. 8. *Gephyromantis ampondo* sp. nov. from Marojejy in life. **A–C.** Male holotype ZSM 402/2016 (MSZC 298) in dorsolateral, dorsal and ventral views; **D.** male paratype ZFMK 59896 in dorsolateral view; **E–G.** male paratype KU 347344 (CRH 1558) in dorsolateral, dorsal and ventral views.

Description of holotype. Specimen in excellent state of preservation, with muscle and skin tissue removed from right thigh for molecular analysis, and skin surrounding left femoral gland partly detached for gland examination (Fig. 9). Snout–vent length 31.7 mm. For other measurements see Table 2. Body slender; head longer than wide, about as wide as body; snout rounded to slightly pointed in dorsal and rounded in lateral view; nostrils directed laterally, protuberant, much nearer to tip of snout than to eye; canthus rostralis distinct, strongly concave; loreal region strongly concave; tympanum distinct, ovoid, higher than wide, its horizontal diameter 45 % of eye diameter; supratympanic fold distinct, regularly bending downwards in its anterior part, subsequently running straight towards the forelimb insertion; tongue ovoid, distinctly bifid posteriorly; vomerine teeth distinct, in two small rounded aggregations, positioned posteromedial to choanae; choanae rounded; maxillary teeth present. Weakly distinguishable, small, slightly dark dermal fold (indicating inflatable skin of the vocal sac) in the extreme posterolateral corners of the throat. Arms slender, subarticular tubercles single; outer metacarpal tubercle very poorly developed and inner two (partly fused) outer metacarpal tubercles relatively well developed; fingers without webbing; relative length of fingers 1 < 2 < 4 < 3, second finger distinctly shorter than fourth; finger discs distinctly enlarged, nuptial pads absent. Hindlimbs slender; tibiotarsal articulation reaching just beyond snout tip when hindlimb is adpressed along body; lateral metatarsals separated by webbing; inner metatarsal tubercle distinct, outer metatarsal tubercle small but recognizable; webbing formula of foot 1 (1.5), 2i (1.5), 2e (1), 3i (2), 3e (1), 4i (2.5), 4e (2.25), 5 (1); relative toe length 1 < 2 < 3 < 5 < 4; fifth toe slightly longer than third toe; toe discs distinctly enlarged. Skin dorsally rather granular, with a pattern of rather irregular but distinct longitudinal ridges. Two distinct inter-ocular

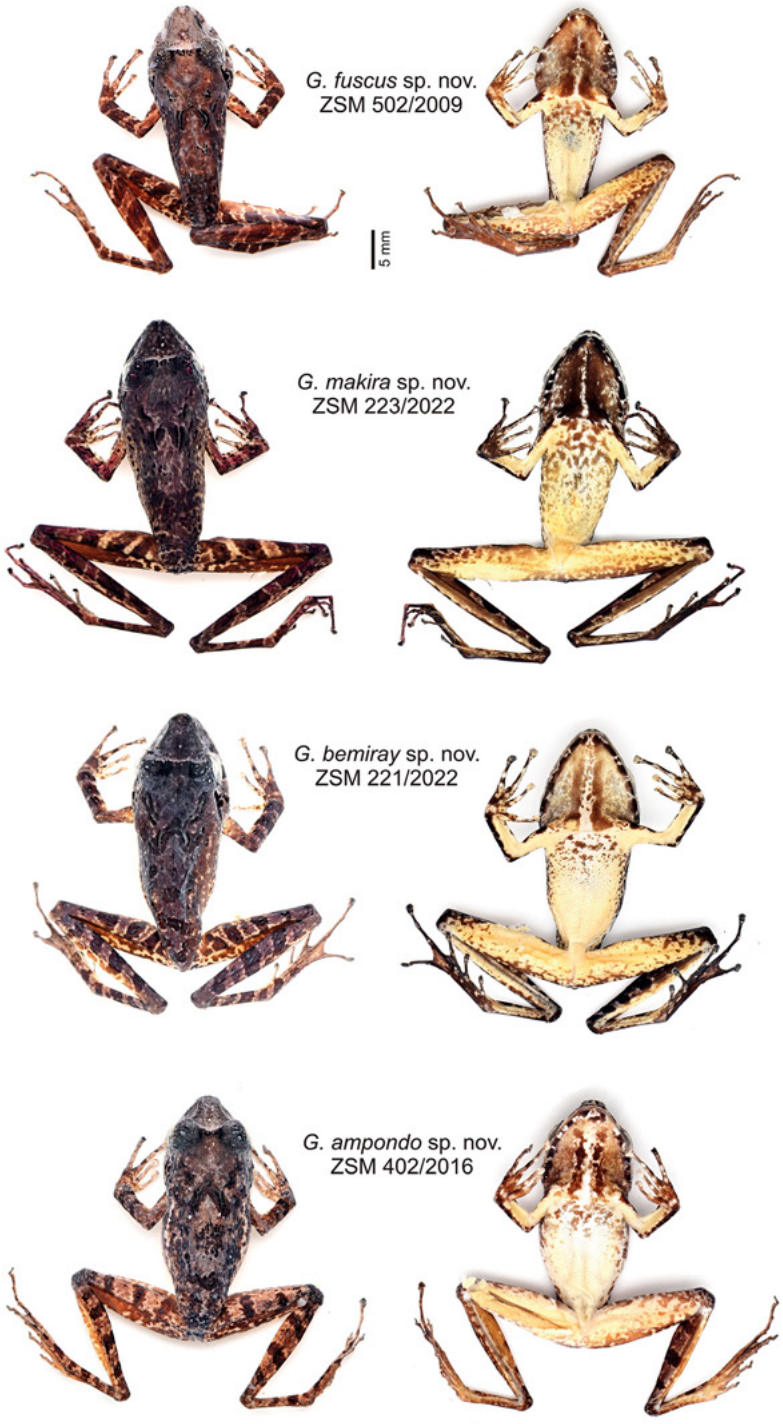

Fig. 9. Preserved name-bearing holotypes of the four species of the *Gephyromantis moseri* complex described herein in dorsal (left) and ventral (right) views.

tubercles. Numerous supraocular tubercles, not truly spine-like. Ventral skin smooth on throat, chest, and limbs, granular on posterior portion of abdomen. Femoral macroglands of type 2 (sensu Glaw et al. 2000) well delimited externally, consisting of about 18 small separate gland granules on the right side.

After 7 years of preservation in ethanol, dorsally brown with irregular and poorly defined lighter and darker markings. The dorsolateral ridges are outlined in a weakly delimited dark brown colour. A dark brown bar runs between the eyes, and anterior to this bar, the colour on the dorsal surface of the head is light-brown to beige. Head laterally light brown to beige, with dark spotting and a pattern of alternating dark and light vertical bars on upper and lower lip. Flanks cream with brown mottling. Hindlimbs with about four relatively well delimited dark brown crossbands both on shank and thigh, upper arm with three dark crossbands. Ventrally cream, with some brown mottling on limbs and chest, and dense brown pigmentation on throat; a broad medial light stripe delimited by strongly contrasted brown colour on chest and throat. Colour in life was similar to that in preservative but overall more contrasted. Ventrally, the belly and the medial stripe on throat were white, femoral glands were light brownish with orange-yellow shade. Eyes in life had grey-cream colour ventrally on iris, more yellowish-beige on the dorsal part, with a very slight reddish shade laterally.

Etymology. The name is derived from the Malagasy word "ampondo", meaning "horns" in Sakalava dialect, and making reference to the interocular tubercles of this species which (even if less expressed than in other similarly named *Gephyromantis* such as *G. cornutus* and *G. tandroka*) are reminiscent of tiny horns. The name is used as a noun in apposition.

Variation. Measurements of two paratypes from Marojejy are included in Table 2. SVL is 29.0–31.7 mm in males (including the holotype). None of the paratypes has a colour pattern conspicuously deviating from the holotype.

Natural history. At Marojejy, specimens were collected at night, on perches of 1–2 m above the ground in low-elevation rainforest, at some distance from a small stream. They were not heard calling.

Distribution. The species is known from Marojejy National Park (near camps "0" and "Mantella"). The known elevational range occupied by the species is around ca. 300 m a.s.l.

Discussion

This study contributes to completing the inventory of the subgenus *Duboimantis* by adding four new species. The majority of *Duboimantis*, and many of the recently discovered species (Scherz et al. 2017b, 2018a), occur in northern Madagascar (delimited by a diagonal spanning from 15.5° S on the east coast to ca. 15.0° S on the west coast; Brown et al. 2016), where the center of diversification of the group has also been reconstructed (Kaffenberger et al. 2012). The *G. moseri* complex is represented by *G. ampondo* and *G.* sp. Ca19 in northern Madagascar (specifically in the North East region), whereas *G. makira*, *G. bemiray* and *G.* sp. Ca33 occur just along its southern limits (at the boundary between the North East and the Northern Central East regions). Although our molecular analyses are only based on short DNA fragments and were not designed to reliably reconstruct phylogenetic relationships, they indicate that the two species with the southernmost ranges (*G. moseri* and *G. fuscus*) are closely related to each other, i.e., forming a clade along with *G.* sp. Ca33 that is nested among most other species. This agrees with the hypothesis of a northern origin also of the *G. moseri* complex, with subsequent dispersal and diversification into the Northern Central East.

Several species of *Duboimantis* are relatively widespread, with ranges encompassing both the Northern Central East and North East such as for instance *Gephyromantis luteus* and *G. redimitus*. Despite substantial genetic divergence among populations, current evidence suggests these should best be considered as conspecific (Rodríguez et al. 2015, Vences et al. 2021b). On the contrary, other *Gephyromantis* subgroups such as the *G. malagasius* complex in the subgenus *Laurentomantis*, or the *G. boulengeri* complex in the subgenus *Gephyromantis*, contain various species occurring allopatrically or parapatrically in the Northern Central East, differing primarily in bioacoustics (Vences et al. 2022, Miralles et al. 2023). The *G. moseri* complex appears to rather follow this second pattern, and more extensive surveys are needed to understand if the different species in the complex are specialized to different elevations, as is the case in the *G. malagasius* complex (Vences et al. 2022). Current data (see Distribution sections in species accounts) indicate that several species occupy rather large elevational ranges (from sea level to 900 m a.s.l. in *G. bemiray*) and therefore do not support a clear elevational segregation.

At present, *G. moseri* is assessed as Least Concern in the IUCN Red List (IUCN SSC Amphibian Specialist Group 2016). This assessment was based on the assumption of a widespread species, ranging from Andasibe to Marojejy, and the associated

map even showed a range reaching northwestwards into the Sambirano region (probably due to unpublished data made available for the assessment). After splitting *G. moseri* into five species, several of these show rather restricted ranges, and may qualify for a threatened category following IUCN criteria (IUCN 2001), considering the current high rates of deforestation in Madagascar, including protected areas (Suzzi-Simmons 2023). As far as is known, all nominal species of the complex occur in at least one protected area: *G. moseri* in Mantadia-Analamazaotra National Park near Andasibe and in Betampona Special Reserve, *G. fuscus*, *G. makira* and *G. bemiray* in Makira Reserve, and *G. ampondo* in Marojejy National Park, but an ongoing reduction of habitat is probable for several of these species (e. g., the Mahasoa forest fragment where *G. fuscus* was collected in 2008 has likely been completely destroyed since then), and even in many protected areas, anthropogenic pressure on the forests is high. However, it also needs to be taken into account that species of the *G. moseri* complex are not easily observed and/or identified, as is evident from very few records referable to *G. ampondo* despite multiple herpetological surveys carried out in the Marojejy Massif, and just a single observation identified as *G. moseri* out of 541 *Gephyromantis* observations on iNaturalist as of 16 September 2023 (https://www.inaturalist.org/observations/28391976, assignable to *G. bemiray*). As discussed by Vences et al. (2022), reliably assessing population trends for such low-density species is inherently difficult. In any case, our study emphasizes the importance of Makira (Parc Naturel de Makira, created as protected area in 2012; Goodman et al. 2018) for the conservation of Madagascar's biodiversity, given that three of the newly described species are known from this reserve and one of these (*G. makira*) has not yet been found anywhere else. Conservation of this reserve, with 374000 ha (Goodman et al. 2018) one of the largest remaining blocks of rainforest in Madagascar, is therefore of high priority.

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